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Mycorrhizae and Reclamation of Stressed Terrestrial Environments

ROBERT M. DANIELSON / *The University of Calgary, Calgary, Alberta, Canada*

I. INTRODUCTION

Studies of mycorrhizal relationships on mine spoils and tailings have spanned nearly two decades. In most instances, the mycorrhizal status of plants growing on mine spoils has been of concern, whereas only relatively few evaluations of the actual effects of the plant-fungus symbioses on plant growth and survival have been made. The essential nature of mycorrhizae for the successful colonization of certain mine wastes was established by the landmark work of J. R. Schramm in the early 1960s. Since that time, research has been expanded to include vesicular-arbuscular (VA) and ericoid mycorrhizae and the development of techniques for inoculating hosts with fungi specifically adapted to spoils. In spite of these advances, mycorrhizal aspects of revegetation programs remain largely in an experimental phase. Reclamation of mined land requires innovative techniques that reduce costs and increase the chance of success of plant establishment and survival. Understanding the role of mycorrhizal associations in relation to establishment and development of plant communities may offer solutions to some of the problems encountered in operational reclamation programs.

Previous reviews (Meyer, 1973; Marx, 1975, 1980a,b; Jurgensen, 1978; Parkinson, 1979) have stressed the difficulties of establishing plants on spoils and tailings due to poor physical and chemical conditions, the lack of organic matter, and often the presence of extremes in temperature and pH. Although these factors are evident to individuals working in revegetation programs, the biological properties, especially mycorrhizal potential, are much less appreciated. The purpose of this review is to update the previous reviews and to determine if mycorrhizae are indeed successful at overcoming the variety of stresses encountered by plants being established or functioning on mine wastes.

II. MECHANISMS BY WHICH MYCORRHIZAE MAY ALLEVIATE STRESS ON MINE SITES

Schramm (1966) has convincingly shown that two factors were essential for vegetation to become established on barren, black coal wastes in Pennsylvania. First, the young seedlings had to be protected from the extremely high surface temperatures to prevent heat girdling of stems, and second, that the plants had to become mycorrhizal to increase their ability to exploit the spoil for nitrogen. Given these circumstances, woody plants did survive and were able to colonize the spoil habitat successfully. Since his work, it has become apparent that other spoil types exert different demands on colonizing plants, and that mycorrhizae can have other benefits beyond scavenging impoverished substrates for their meager supplies of available nitrogen. Some of these mechanisms are well established and others are more speculative, awaiting carefully controlled and analyzed experimentation to be properly evaluated.

It is now recognized that nutrients other than nitrogen may be limiting on mine spoils and that mycorrhizal associations provide an elegant adaptation alleviating deficiencies encountered by potentially mycorrhizal plants. Foremost among these is the enhanced ability of mycorrhizal plants, especially VA mycorrhizal species. to obtain available phosphorus from soils (Malajczuk and Lamont, 1981). Although suggestions have been made to the contrary, evidence now indicates that mycorrhizae are not capable of utilizing sources of phosphorus unavailable to nonmycorrhizal roots but are simply exploiting a larger pool of labile phosphorus (Malajczuk and Lamont, 1981; Smith, 1980; Thomas et al., 1982).

The uptake of nutrients other than phosphorus may also be enhanced by the mycorrhizal condition but evidence is scanty. This enhanced nutrient uptake would be most likely to occur with poorly mobile ions such as zinc and copper and to a lesser extent, ammonium (Lambert et al., 1979; Bowen and Smith, 1981). Bowen and Smith (1981) have pointed out that with less mobile ions, transfer through soil limits nutrient uptake by plant roots, and rooting density and geometry determines total uptake. It would be expected that mycorrhizae would most enhance the uptake of these ions. The degree of development of external mycelium may be of prime importance in the stimulation of host growth. Graham et al. (1982) have shown that for five *Glomus* species, differences in host growth enchancement were related to the amount of extramatrical mycelium produced. This may also be true of ectomycorrhizae, with mycelial strands and rhizomorphs having special importance (Bowen, 1973; Marx, 1980b).

Related to nutrient uptake are the effects of mycorrhizae on the accumulation or exclusion of toxic elements (Smith, 1980). It has often been stated that mycorrhizal plants may be more tolerant to heavy metals than their nonmycorrhizal counterparts but until recently, evidence to support this contention has been lacking. Bradley et al. (1981) pointed out that whereas enhanced uptake of ions such as phosphorus by mycorrhizae is beneficial, increased uptake of heavy metals may be very deleterious to plant growth and survival in soils containing high concentrations of metals. In field soils, it has been shown that mycorrhizae substantially increase the uptake of copper and zinc, both in terms of total uptake and concentration in the tissues (Lambert et al., 1979). This suggests that the mycorrhizal condition of plants on areas contaminated with copper, zince, and other heavy metals, as well as on acid soils where aluminum toxicity may be a problem (Brady, 1974), could influence plant growth and perhaps the types of plants present.

Bradley et al. (1981, 1982) studied the tolerance of ericaceous plants and their endophytes from contaminated and normal soils to various concentrations of copper and zinc in sand cultures. In all cases, the growth of mycorrhizal plants was superior to the growth of nonmycorrhizal plants when exposed to either copper or zinc. Tolerance to copper and zinc occurred regardless of the origin of the host or the endophyte. It appeared that protection was due to the restriction of translocation of the metals from roots to shoots with the metals accumulating in the roots. Bradley et al. (1981) suggest that protection is afforded by the adsorption of ions on the cell wall of the hyphae in the root and, further, that plants with VA mycorrhizae would be less tolerant due to less biomass of internal hyphae and the phycomycetous nature of the endophyte. This suggestion has been substantiated by a preliminary report by Killham and Firestone (1982). They reported that mycorrhizal grass plants were more sensitive to copper and nickel and had higher metal concentrations in the shoots than nonmycorrhizal plants. Although additional studies are required, these results imply that VA mycorrhizal plants are poorly adapted to sites with high levels of toxic metals. It would seem likely that ectomycorrhizal plants would behave similarly to ericaceous plants, in that mycorrhizae have a large fungal biomass component and thus large adsorptive surfaces. An organism such as the E strain, which produces intracellular infections in pine (Mikola, 1965), might be particularly effective in ameliorating the effects of heavy metals.

Another factor that has been repeatedly cited as a critical factor of revegetation of mine spoils, and one that might be alleviated by mycorrhizae, is drought tolerance. However, the opinion expressed by Powell (1982) was that conclusive evidence showing that mycorrhizal infection of plants results in increased water uptake is lacking. Most frequently, the work by Safir et al. (1972) has been cited as demonstrating the beneficial effect of mycorrhizae on the water relations of plants. They reported reduced resistance of water transport in mycorrhizal soybean roots as compared with nonmycorrhizal roots. In a separate experiment, the addition of a complete nutrient solution eliminated the differences in resistance between inoculated and noninoculated plants (the roots were not examined for infection) suggesting the mycorrhizal effect was simply due to more favorable nutrition. However, it should be kept in mind the technique used by Safir et al. (1972) to determine resistances involved saturating the soil (Boyer, 1971) and thus did not account for soil or rhizosphere resistance to water movement. As VA mycorrhizae are known to enhance phosphorus uptake by more effective exploitation of the soil than possible with nonmycorrhizal plants, possibly the most likely function of mycorrhizae in water relations (increased utilization of water distant from the rhizosphere) may have been overlooked. In a study of *Pinus radiata*, Sands and Theodorou (1978) concluded that soil resistance was a more important factor in water relations than plant resistance. This would suggest that root distribution and the nature of the extramatrical mycelium might be as important for water uptake as for uptake of poorly mobile ions. Allen (1982) showed that mycorrhizal infection of the grass *Bouteloua gracilis* reduced soil resistance as well as within-plant resistances and proposed that the improved water relations might be an important factor in plant survival in arid habitats. In contrast, Sands and Theodorou (1978) found that mycorrhizal infection of *Pinus radiata* with *Rhizopogon luteolus* resulted in increased within-plant resistance and increased water stress. These apparently conflicting results indicate that caution should be exercised in attributing mycorrhizae with the property of increasing drought tolerance until field or greenhouse studies actually demonstrate that infected plants survive and reproduce better than noninfected plants when under water stress.

Goss (1960) conducted one of the few tests to determine if mycorrhizae would influence drought tolerance. *Pinus ponderosa* is used in shelter belts in the Great Plains where rainfall is low, and Goss felt that the presence of mycorrhizae might be critical for survival of planting stock. Pot experiments were conducted with mycorrhizal and nonmycorrhizal seedlings and water was withheld until the seedlings exhibited drought symptoms followed by water addition and monitoring of recovery patterns. The water stress in all cases was severe and in three tests all the seedlings died. In a fourth test, 4 of 30 mycorrhizal seedlings died and 12 of 29 nonmycorrhizal seedlings died. Goss attributed the differences in survival to the better poststress lateral root development of the mycorrhizal seedlings, which in turn may have been due to the greater size and vigor of the mycorrhizal plants. Thus, in a test of a sudden and severe water deficiency, Goss' work indicates that mycorrhizal plants may survive better than nonmycorrhizal plants, but this may be due to seedling vigor rather than a direct mycorrhizal effect. A preliminary report by Duddridge et al. (1980) states that *Pinus* *sylvestris* seedlings infected with *Suillus bovinus* were able to survive a dry period whereas uninfected seedlings died, the mycorrhizal seedlings were able to obtain water from distant wet soil via transport through a system of rhizomorphs. This strongly indicates that rhizomorphic ectomycorrhizal species may increase drought tolerance by allowing exploitation of larger soil volumes than nonmycorrhizal seedlings or mycorrhizal plants lacking rhizomorphs. It remains to be shown that the mycorrhizal status per se improves plant water relations and drought tolerance under field conditions.

Mine spoils may also be extremely acidic (Jurgensen, 1978) and have high surface temperatures. Schramm (1966) found the surface temperatures on black coal wastes frequently reached 40—60°C and occasionally reached 75°C. It is expected that temperatures in the root zone of mine sites would substantially exceed root zone temperatures in undisturbed areas where the vegetation would reduce insolation. Thus, indigenous fungi may not be adapted to postdisturbance temperature regimes. However, few studies have compared mycorrhizal associations (as opposed to pure culture studies) over a range of temperatures. Marx et al. (1970) and Marx and Bryan (1971) demonstrated in monoxenic culture that not only could *Pisolithus tinctorius* infect roots at higher temperatures than *Thelephora terrestris*, but that the tolerance of the pine seedlings to high temperatures was increased considerably when infected with *Pisolithus*. Similar experiments have not been performed with other fungi or in open systems where the humidity is low and concurrent demands are placed on water uptake.

Nonlethal temperatures also affect mycorrhizal development with substantial differences existing among species and strains (Theodorou and Bowen, 1971; Schenck and Smith, 1982). Colonization and infection of roots by certain species of VA fungi has been shown to be slow at 18°C (Schenck and Smith, 1982) and at 16°C for ectomycorrhizal fungi (Theodorou and Bowen, 1971), temperatures that may be well above those normal in temperate regions (Theodorou and Bowen, 1971). Thus, if mycorrhizal associations are to be manipulated on disturbed sites, temperature relations may be a critical factor in symbiont selection (Trappe, 1977).

The effects of soil pH on the development of mycorrhizae have been reviewed several times, e.g., Slankis (1974) and Mosse et al. (1981). From these reviews it appears that individual species of endophytes can form mycorrhizae over a wide pH range and that mycorrhizae develop with appropriate host plants at any soil pH were the host occurs. However, the symbionts of both VA and ectomycorrhizae probably differ in extremely acid or alkaline soils from soils with moderate pH values, with few species being involved at the extremes (Trappe, 1977). The high solubility of potentially toxic heavy metals (Jurgensen, 1978) is related to low pH levels the possibility of micronutrient deficiences is related to high pH values.

III. MYCORRHIZAL SYMBIONTS INDIGENOUS TO MINE SPOILS

From the restricted number of published reports, the number of fungal symbionts reported to occur on mine spoils is low (Table 1). The limited number of observations, as well as the risk of relating fruit body occurrence with mycorrhizal abundance, makes a conservative interpretation of the data essential. Reports of gasteromycetes and hymenomycetes with persistent fruit bodies have been numerous but, with the exception of *Pisolithus tinctorius*, there is little evidence that these fungi are dominant symbionts on mine spoils. Due to the bright yellow color of the mycelium of some strains of *P. tinctorius*, it can be readily recognized, unlike most other ectomycorrhizal fungi. Schramm (1966) observed the natural infection of a variety of woody plants by *Pisolithus* and described in detail the penetration of the spoil and cracks of shale by the yellow rhizomorphs. Schramm showed conclusively that *Pisolithus* naturally colonized roots in barren spoils and developed an extensive system of mycelium and rhizomorphs. No other fungus has been assessed quantitatively for actual mycorrhizal abundance on mine spoils. The collection data suggest however that few agarics fruit on spoils and only a few species may be involved in mycorrhizal associations on barren spoils. *Inocybe* and *Laccaria* appear to be two genera containing species capable of forming mycorrhizae on barren spoils whereas Schramm (1966) found *Amanita*, *Cenococcum*, and *Boletus* only associated with older trees where a litter layer had developed. However, Benson et al. (1980) reported five genera in the Agaricales fruiting on largely uncolonized arsenic mine wastes.

Ascomycetes appear to be rare as ectomycorrhizal symbonts with the possible exception of E-strain fungi. Since a teleomorph is unknown for the E strain, its presence must be determined by direct examination of the mycorrhizae. E-strain fungi may be the dominant symbionts in nurseries in north temperate regions (Laiho, 1965; Mikalo, 1965) as well as in tropical regions (Mikola, 1980), a situation similar to that found with *Thelephora terrestris*. It would appear likely that E-strain fungi could be readily introduced with planting stock into minespoils, although observations indicate that E-strain fungi do not persist after outplanting (Mikola, 1965; Thomas and Jackson, 1979). However, mine spoils may offer little competition from indigenous fungi and E-strain fungi have been observed to be the dominant symbionts of white spruce in a coal mine spoil for a period exceeding 4 years (Danielson, unpublished data).

The inclusion of *Helvella corium* and *Sepultaria arenose* [*Geopora arenicola* (Lev.) Kers] is provisional because Schumacher (1979) reports both species to fruit in open areas. However, other species of *Geopora* are almost certainly mycorrhizal (Trappe, 1971) and the possibility of these ascomycetes forming mycorrhizal associations deserves further attention.

The ascomycete *Pezizella ericae* and perhaps close relatives are the only recognized fungal associates of ericoid mycorrhizae (Read, 1974; Mosse et al., 1981). As ericaeous plants are the dominant colonizers of spoils containing excesses of heavy metals (Bradley et al., 1981), it is certain that *Pezizella* is an important endophyte on mine spoils.

VA mycorrhizal endophytes differ from ectomycorrhizal fungi in many ways but prominent among the general differences are taxonomic, lack of host specificity, slowness of dispersal, and the small number of species of the VA fungi. The species spectrum found on mine spoils is not unlike that reported for undisturbed habitats (Gerdemann and Trappe, 1974), indicating a lack of selection or adaptation to spoils at the species level. In general, Mosse et al. (1981) observed that most VA fungal species were worldwide in distribution but that within a small distance spore populations may be highly variable and dependent upon the host species. Thus, one might not expect distinct groups of species on mine spoils owing to the poor dispersal mechanisms, the relatively few species available for colonization, and the lack of host specificity. However, intraspecific adaptation to the spoil environment may occur as illustrated by the much greater tolerance to zinc and cadmium of a strain of *Glomus mosseae* from a site polluted with zinc and cadmium as compared with a strain from a field soil (Gildon and Tinker, 1981). Strain adaptation to other extreme features of mine spoils, e.g., temperature, probably also occurs and may be as important as differences among species.

IV. MYCORRHIZAL DEVELOPMENT ON MINE SPOILS AND TAILINGS

A majority of the mycorrhizal studies on mine spoils have been conducted either to determine the presence or absence of mycorrhizae or to monitor the development of mycorrhizal root systems with time. These studies imply that there are beneficial effects of infection, but unaided by supplemental studies, they do not prove it. Schramm (1966) found nearly all the successful colonizers of black coal wastes in Pennsylvania were mycorrhizal. These included species of *Pinus*, *Betula*, *Populus*, and *Salix* and all were ectomycorrhizal. The wastes were 30–36 years old and on some there had been no spontaneous revegetation for 30 years. However, when pine was seeded on these areas and protected from high surface temperatures, the seedlings quickly become mycorrhizal. Schramm concluded that inoculum was abundant and generally not a decisive factor in plant establishment. With the exception of the legume, *Robinia*, which is capable of fixing N_2 when nodulated with *Rhizobium*, VA host plants were generally unsuccessful colonizers. *Acer rubrum* seedlings were occasionally found and were mycorrhizal, but did not live past the second growing season. Schramm's observations suggest that VA plant failure was due to their inability to obtain

Table 1 Mycorrhizal Fungi Reported to Occur on Mine Spots

Mycorrhizal species	Spoil type	Reference
Amanita muscaria (L. ex Fr.) Hooker	Arsenic spoil	Benson et al. (1980)
Amanita rubescens (Fr.) S.F. Gray	Coal spoil	Schramm (1966)
Amphinema byssoides (Fr.) J. Erikss.	Coal spoil	Danielson (unpublished data)
Astraeus hygrometricus (Pers.) Morgan	Coal spoil Slag heaps	Schramm (1966) Gaie and Heinemann (1980)
Boletus sp.	Uranium tailings Coal spoil	Kalin and Stokes (1981) Schramm (1966)
Cenococcum geophilum Fr.	Coal spoil Lignite spoil	Schramm (1966) Mejstrik (1971)
E strain	Coal spoil	Zak et al. (1982)
Helvella corium (Weberb.) Massee	Uranium tailings	Kalin and Stokes (1981)
Inocybe dulcamara (A. & S. ex Pers.) Kummer	Mine waste	Malloch (1982)
Inocybe immigrans Malloch	Uranium tailings Mine wastes	Kalin and Stokes (1981) Malloch (1982)
Inocybe lacera Fr.	Uranium tailings Coal spoil	Kalin and Stokes (1981) Schramm (1966)
Inocybe sp.	Coal spoil	Schramm (1966)
Leccinum scabrum (Bull. ex Fr.) S.F. Gray	Arsenic spoil	Benson et al. (1980)
Laccaria laccata (Scop. ex Fr.) Cooke	Arsenic spoil	Pyatt (1973) Benson et al. (1980)

Laccaria proxima	Uranium tailings	Kalin and Stokes (1981)
Lactarius rufus (Scop. ex Fr.) Fr.	Arsenic spoil	Benson et al. (1980)
Paxillus involutus (Batsch ex Fr.) Fr.	Arsenic spoil	Benson et al. (1980)
	Uranium tailings	Kalin and Stokes (1981)
Pisolithus tinctorius (Pers.) Coker & Couch	Coal spoil	Schramm (1966)
	Coal spoil	Medve and Gill (1982)
	Many spoils (Review)	Marx (1977)
	Nickel tailings	Malloch and Kuja (1979)
Rhizopogon vulgaris	Minespoils	Miller (1982)
Scleroderma aurantium Pers.	Coal spoil	Medve and Gill (1982)
	Coal spoil	Schramm (1966)
	Coal spoil	Meyer (1973)
Scleroderma citrinum Pers.	Arsenic spoil	Benson et al. (1980)
Sepultaria arenosa (Fuckel) Boud.	Uranium tailings	Kalin and Stokes (1981)
Russula sp.	Coal spoil	Medve et al. (1977)
Suillus luteus	Coal spoil	Medve and Gill (1982)
	Coal spoil	Medve et al. (1977)
Suillus tomentosus	Oil sand tailings	Parkinson et al. (1980)
Thelephora caryophyllea Schaeffer ex Fr.	Coal spoil	Schramm (1966)
Thelephora terrestris Ehrh. ex Fr.	Arsenic spoil	Benson et al. (1980)
	Uranium tailings	Kalin and Stokes (1981)
	Coal spoil	Schramm (1966)
	Coal spoil	Medve and Gill (1982)
	Oil sand tailings	Parkinson et al. (1980)
	Coal spoil	Medve et al. (1977)

Table 1 (continued)

Mycorrhizal species	Spoil type	Reference
Tomentella sp.	Coal spoils + peat	Danielson (unpublished data)
Pezizella ericae Read	Metal-contaminated spoil	Bradley et al. (1981, 1982)
Entrophospora infrequens (Hall) Ames & Schneider	Coal spoil	Zak et al. (1982)
"fine endophyte"	Coal spoil	Daft et al. (1975)
	Coal spoil	Lambert and Cole (1980)
	Coal spoil	Daft and Nicolson (1974)
	Coal spoil + peat	Zak et al. (1982)
	Oil sand tailings + peat	Zak et al. (1982)
Gigaspora calaspora	Coal spoil	Daft et al. (1975)
	Coal spoil	Daft and Nicolson (1974)
Gigaspora gigantea	Coal spoil	Daft et al. (1975)
	Coal spoil	Daft and Hacskaylo (1976)
	Spoil + topsoil	Langkamp and Dalling (1982)

Gigaspora gilmoreii Trappe & Gerdemann	Spoil + topsoil	Langkamp and Dalling (1982)
Gigaspora sp.	Spoil + topsoil	Langkamp and Dalling (1982)
Glomus aggregatum Schenck & Smith	Coal spoil	Zak et al. (1982)
	Oil sand tailings	Zak et al. (1982)
Glomus fasciculatum	Stockpile	Rives et al. (1980)
	Coal spoil	Daft et al. (1975)
	Coal spoil	Daft and Hacskaylo (1976)
	Coal spoil	Daft and Nicolson (1974)
	Surface spoil	Bohn and Liberta (1982)
Glomus macrocarpus var. *geospora*	Coal spoil	Daft et al. (1975)
Glomus macrocarpus var. *macrocarpus*	Coal wastes	Khan (1978)
Glomus mosseae (Nicol. & Gerd.) Gerd. & Trappe	Zn-Cd spoil	Gildon and Tinker(1981)
	Coal spoils	Zak et al. (1982)
	Oil sand tailings	Zak et al. (1982)
Sclerocystis rubiformis Gerdemann & Trappe	Coal Wastes	Khan (1978)

sufficient soil nitrogen, as neither water nor phosphorus were limiting and nitrogen-fixing species of *Alnus* and *Robinia* were successful. Furthermore, grasses colonizing the sites responded to ammonium but not phosphate amendments.

The ectomycorrhizae that Schramm described on the spoil were characterized either by extensive rhizomorph development (*Astraeus, Pisolithus, Boletus, Thelephora*) or hyphae which fused soil particles tightly to the mycorrhizal surface (*Inocybe, Boletus*). These mycorrhizal features may represent especially efficient methods of extracting and transferring meager nitrogen supplies to the roots. The adhesion of soil particles to roots in dry soil has been suggested as a mechanism to increase water conductivity (Coutts, 1982) and it may also function to enhance the movement of mobile ions such as nitrate. Hyphae of VA fungi may extend 8 cm from the root surface (Rhodes and Gerdemann, 1975), but rhizomorphs of *Pisolithus* may extend 4 m into the soil (Schramm, 1966), a result that suggests ectomycorrhizae are better adapted to long-distance transport than VA mycorrhizae. Schramm observed that *Astraeus* formed a dense network of rhizomorphs and mycelia near the spoil surface where intermittent drying occurred. He suggested that these fungal structures may survive drying and revive quickly to use nitrogen from precipitation percolating into the spoil.

Studies since 1966 on additional mining wastes have shown colonization patterns of plants and mycorrhizal types differing from those observed by Schramm. Ten-year-old untreated coal tips in Scotland were colonized by both grasses and dicotyledonous plants and all but one species (which was nonmycorrhizal) were infected with VA fungi (Daft and Nicolson, 1974). Extractable phosphorus levels were low (0.3–2.3 μg/g) and the authors considered that successful plant growth was dependent on VA infection and the resulting increase in phosphorus uptake. Similar results were found in coal wastes in Pennsylvania in which 23 of 24 colonizing plant species were VA mycorrhizal (Daft and Hacskaylo, 1976). Some of the same woody nitrogen-fixing plants that Schramm (1966) observed to be successful colonizers (*Robinia hispida, R. pseudoacacia* and *Alnus glutinosa*) were determined by Daft and Hacskaylo (1976) to have VA mycorrhizae. On lignite spoil banks, *Alnus glutinosa* was observed to be ectomycorrhizal (Mejstrik, 1971). Khan (1978) examined plants colonizing three bituminous coal tips in Australia that were composed of mine dirt and washer discard and determined that 22 of 26 species were infected with VA fungi and four were nonmycorrhizal. Spores were extracted from spoil collected from the root zone of all the 26 species.

Plants grown in unamended fresh coal spoils have been observed to become VA mycorrhizal by Ponder (1979), Mott and Zuberer (1982), and Zak and Parkinson (1982). Unlike the examples cited above, some mine spoils have been observed to be noninfective, i.e., devoid of mycorrhizal inoculum. Aldon (1978) planted *Atriplex canescens* in 4-year-old spoil in New Mexico and did not detect any infection in noninoculated seedlings after the second growing season. A 10-year-old Pennsylvania spoil bank used in a field study by Lambert and Cole (1980) was completely noninfective for white clover. The addition of amendments containing inoculum can substantially decrease the delay in infection, and this may be a desirable procedure on some mine spoils or tailings (Zak and Parkinson, 1982). However, Allen and Allen (1980) found that even when stockpiled grassland topsoil was mixed with spoil, infection levels of the grass *Agropyron smithii* were nil or much lower than on undisturbed sites. Even after 3 years, infection levels on reclaimed sites were less than half those on the undisturbed grassland. The low levels of infection may have been due to stockpiling and the incorporation of surface materials from as deep as 2 m. Schwab and Reeves (1981) showed that very little VA inoculum was present below a depth of 0.5 m in an arid sage community. In contrast, however, Lambert and Cole (1980) obtained high levels of infection of white clover after one growing season on spoil amended with topsoil from a grassy field. Three legumes responded well to the addition of soil but grasses did not show a response that could be attributed to mycorrhizal status. Lambert and Cole (1980) did not examine the roots of the grasses for infection, but it may be that the grasses were infected less than the legumes and were more sensitive to low inoculum levels.

The harsh procedures used to remove bitumen from sand mined in northern Alberta results in mine tailings that are completely devoid of mycorrhizal inoculum (Parkinson, 1979). To obtain early establishment of mycorrhizae, inoculum must be introduced to tailings of this type. Zak and Parkinson (1982) found that less than 1% of slender wheatgrass roots grown in untreated sand were infected after one growing season, whereas tailings amended with peat from a forested site resulted in 23% infection. After 2 and 4 years, infection of slender wheatgrass roots in untreated sand reached 4% and 36%, respectively, illustrating the extremely slow introduction of effective inoculum via wind, water, or animal transport even though the experimental plots were surrounded by pastures (Zak and Parkinson, 1983). The addition of a mineral fertilizer to the tailings sand resulted in much larger root systems but did not result in a percent increase in infection although the infected root length of fertilized plants was greater after 2 years than plants in unamended tailings. The fertilizer level used was not high enough to suppress infection because mycorrhizae formed readily on slender wheatgrass in adjacent coal mine spoil test plots (Zak and Parkinson, 1982).

The source or quality of ectomycorrhizal inoculum can influence the rates of mycorrhizal development on roots growing in tailings sand. Containerized jack pine seedlings that were infected with *Thelephora terrestris* were also grown on the experimental plots described by Zak and Parkinson. Although *Thelephora* is thought to be highly aggressive, insignificant root colonization occurred in tailings sand after one growing season (Parkinson et al., 1980). In peat-amended sand, 25% of the short roots were infected by E-strain fungi indigenous to the peat (Danielson, 1982). After two seasons' growth, infection by *Thelephora terrestris* in untreated and fertilized tailings sand did not exceed 33% whereas in the peat-amended tailings infection by E-strain reached 72%. These studies on slender wheatgrass and jack pine illustrate the slow establishment of mycorrhizae in spoils devoid of inoculum. The introduction of effective inoculum may be beneficial, as Mosse et al. (1981) state that the seedling stage may be the most mycorrhizal dependent stage both for tree species and VA annuals. Furthermore, Abbott and Robson (1981) conclude that the rate of mycorrhizal formation is particularly important with annuals grown in areas with short growing seasons.

The pioneer plants colonizing disturbed areas and spoils in the arid southwestern U.S. have been observed to be largely nonmycorrhizal annuals (Reeves et al., 1979; Miller, 1979; Allen and Allen, 1980). Reeves et al. (1979) studied the mycorrhizal status of plants colonizing a road bed abandoned 3 years previously and an adjacent sage community. Their results showed that the road bed was dominated by nonmycorrhizal plants (99% plant cover by *Salsola kali*) whereas nonmycorrhizal plants were rare in the undisturbed community. The authors suggested that the presence of nonmycorrhizal species may be detrimental to the establishment of mycorrhizal-dependent species by reducing inoculum levels in disturbed soils. The disturbed soil was far less infective than the undisturbed soil (Moorman and Reeves, 1979), but it was not shown that inoculum levels were so low as to prevent establishment of mycorrhizal species. Miller (1979) observed a similar phenomenon on spoil covered with 30 cm of topsoil as compared with undisturbed plant communities. No mycorrhizae were detected on the disturbed site although viable inoculum was present and some species on the disturbed site were mycorrhizal in the native sites. Allen and Allen (1980) also observed the dominance of nonmycorrhizal species on some mining sites treated with stockpiled topsoil. In a disked area dominated by the nonmycorrhizal species *Chenopodium pratericola* and *Salsola kali*, the infection of roots of *Agropyron smithii* exceeded 62% 1 and 2 years following disturbance.

It remains to be determined if indeed the presence of weedy nonmycorrhizal annuals inhibits the establishment of mycorrhizal species by reducing soil infectivity or if other factors are responsible for the success of these plants. In any case, many of these species are autoallelopathic, e.g., *Kochia scoparia* and *Salsola kali*, and thus usually disappear rapidly (Lodhi, 1979a,b). Mosse et al. (1981) have also stated that such species are opportunistic and thus inherently less competitive than mycorrhizal species that follow in the successional sequence.

Although stockpiling and replacement of topsoil is often required by legal regulations and is desirable for plant establishment, the question has been raised whether the practice has unfavorable effects on mycorrhizal inoculum and hinders plant establishment. Two methods have been used to determine the effects of stockpiling on VA mycorrhizal inoculum, spore counts and a greenhouse bioassay utilizing a rapidly growing test plant. Spore counts have been shown to provide an unreliable index of soil infectivity (Abbott and Robson, 1981; Gould and Liberta, 1981) and the corn bioassay is considered to provide a better indication of the presence of total infective propagules (Moorman and Reeves, 1979; Gould and Liberta, 1981). In a similar manner, the infective potential of forest soils subjected to disturbances (Schoenberger and Perry, 1982) and of oil sand overburden materials (Danielson et al., 1983) have been evaluated.

Stockpiling of topsoil for up to 3 years has been shown to have no effect on rates of infection after 1 month when undiluted soil was used (Rives et al., 1980). After 4.5 years, infection had decreased from 93% to 80% (Gould and Liberta, 1981). Using a series of different aged stockpiles, Liberta (1981) estimated that infectivity of undiluted soil decreased from 85% to 12% after 3 years. When the soil was diluted with an inoculum-free medium, the effect of stockpiling on reducing viable mycorrhizal inoculum was much more evident. There is little doubt that stockpiling will result in decreased infectivity of topsoil but the studies conducted so far have failed to demonstrate that the decreases will significantly affect plant growth and survival.

In the reclamation of extracted oil sands, amendation is absolutely necessary (Parkinson et al., 1980). The amendments will be the sole sources of plant nutrients, organic matter, and mycorrhizal inoculum except for slow introduction slowly by wind and precipitation. The principal amendment used is stockpiled peat from black spruce-tamarack muskeg sites. Due to the critical nature of the amendment characteristics used on mine tailings, such as oil sands and retorted oil shale, the amendments should be carefully evaluated for mycorrhizal inoculum. Danielson et al. (1983) examined several potential oil sand amendments for mycorrhizal infectivity and found that peat contained very small quantities of VA mycorrhizal inoculum, as indicated by infection levels of slender wheatgrass plants grown in the greenhouse. However, substantial quantities of VA inoculum were present at 1-m depths in mixed forest stands, and this material could conceivably be used as a source of VA inoculum in operational procedures. Ectomycorrhizal inoculum compatible with jack pine was present in the peat as well as in soils from the mixed stands with the dominant symbiont being identified as the E strain. Fungi forming mycelial strands were rare and this could indicate that these materials may not provide the most effective symbionts (Marx, 1980b).

V. BENEFITS OF MYCORRHIZAL ASSOCIATIONS ON MINE WASTES

Relatively few studies have shown unequivocal benefits of mycorrhizae on mine spoils. Data from some studies are difficult to interpret due to the lack of thorough quantification of mycorrhizal status of the root system, the failure to determine the persistance of introduced symbionts, or the lack of a sound statistical experimental design. The benefits of mycorrhizae on mine spoils need to be clearly shown to be substantial to alter policies and mining practices that are primarily concerned with moving huge masses of material at high expense. Regardless, several studies have demonstrated that the mycorrhizal symbiosis may provide a valuable and practical tool for achieving the desired end point of reclamation practices on mining wastes.

Schramm's (1966) detailed studies of volunteer and planted woody plants on black mine wastes in Pennsylvania were the first to indicate that mycorrhizae were not only beneficial but essential for plant growth on certain mine wastes. He selected two types of materials, black shale mixed with coal waste and fine grained sludge, both of which supported very sparse vegetation or were entirely barren. The spoils were 30–36 years old, acid, and with surface temperatures exceeding 60°C during the summer on level locations. Schramm determined that it was the high surface temperatures and not acidity or lack of moisture, that prevented the initial establishment of plants. Once established, nonmycorrhizal plants (mostly pines) became chlorotic and eventually died whereas all of hundreds of healthy individual plants he examined were ectomycorrhizal. The predominant mycorrhizal symbiont was *Pisolithus tinctorius*, which could be identified by the bright yellow color of the mycelium. Through irrigation and fertilizer experiments, Schramm established that nitrogen was the decisive factor limiting seedling growth. Phosphorus additions did not relieve deficiency symptoms and combining nitrogen and phosphorus was no better than nitrogen alone. Nonmycorrhizal seedlings responded to nitrogen additions, but after fertilization was terminated growth stopped and deficiency symptoms reoccurred. Reclamation of these black coal wastes with nonnitrogen-fixing plants was only possible by altering the microenvironment around seedling stems and by the establishment of ectomycorrhizal fungi on the seedlings' root systems.

The major advance made since 1966 for the practical application of Schramm's observations has been the development of procedures for producing seedlings inoculated with specific fungi by Marx and coworkers. They recognized that *Pisolithus tinctorius* was particularly well adapted to the harsh environments encountered on mine wastes in the southeastern United States (Marx, 1975) and have shown the practical advantages of using planting stock inoculated with *Pisolithus* (Marx, 1980a,b). Berry and Marx (1978) outplanted *Pinus taeda* and *Pinus virginiana* seedlings inoculated with *Pisolithus* or naturally infested with *Thelephora terrestris* on acid, barren, metallic mine wastes in which previous reforestation attempts had largely failed. After 2 years, seedlings inoculated with *Pisolithus* were significantly larger than the naturally infested seedlings on one of the two sites, with high rates of survival in all treatments. Both *Pisolithus* and *Thelephora* persisted and colonized new roots. On acid coal mine spoils, Marx and Artman (1979) found similar results, with *Pisolithus*-infected seedlings exhibiting both better survival and growth after 3–4 years than seedlings infected with *Thelephora*. In this study, based on visual identifications, *Thelephora* did not appear to persist as well as *Pisolithus*. In another study on coal spoils in the southeastern United States, Berry (1982) demonstrated that container-grown pines planted on spoils untreated in any way other than contouring grew successfully and that inoculation with *Pisolithus* stimulated growth. All of these studies by Marx, Berry, and Artman show a clear benefit in growth performances of inoculation with a specific symbiont. Although the studies did not compare mycorrhizal with nonmycorrhizal plants, they represent a comparison of experimental inoculation with operational forestry practices in the southeastern United States were seedlings became infected with the weedy species *Thelephora terrestris*. Comparisons in northern climates where other fungi [e.g., E strain (Laiho, 1965; Thomas and Jackson, 1979) *Inocybe lacera* or *Laccaria laccata* (Trappe and Strand, 1969; Sinclair, 1974)] may be the dominant nursery fungi are required to determine the fungi of choice in these regions.

The study by Grossnickle and Reid (1982) illustrates some of the difficulties of testing symbiont efficiency with slow-growing hosts in a cold climate with a short growing season, a situation quite unlike that encountered by Marx and his colleagues. An initial problem confounded interpretation of field data in that the intended mycorrhizal-free control and a portion of the inoculation treatments became infected with a greenhouse contaminant. This precluded a determination of the essentiality of the mycorrhizal condition but may have better represented operational conditions. Seedlings of *Pinus contorta*, *Pinus flexilis* and *Picea engelmannii* were inoculated with *Pisolithus tinctorius*, *Suillus granulatus*, and *Cenococcum geophilum* and outplanted on a molybdenum tailings pond covered with alkaline waste rock. Phosphorus, phosphorus plus nitrogen, and sewage sludge plus wood chips were added to some treatments to ameliorate the poor physical and nutritional conditions of the spoil. Regardless of treatment, growth of all three conifer species was minimal for the first 2 years in the field. Height response to sewage sludge as compared with the other amendments was observed in the third year with *P. flexilis* and after 4 years by all three species. The maximum annual height increase was less than 1 cm for the first 2 years and less than 5 cm after 4 years. Height growth appeared to be enhanced by inoculation with *Suillus granulatus*, but again differences in height growth were very small. From the results of Grossnickle and

Reid (1982) it appears that detection of a growth response at such sites will be much more difficult than in warm climates and will require increased times.

In warm climates with fast-growing host species height and stem diameter measurements appear to be adequate for determining response to mycorrhizal inoculum, but it appears unlikely that these measurements are sensitive enough to be used with slow growing species. In a continuation of the amendation experiments on coal spoils described by Zak et al. (1982), no differences in the height growth of white spruce could be detected for one to 4 years among spoils treated with peat, sewage sludge, fertilizer, in comparison with controls (Danielson et al., 1979 and unpublished data). It was not until after the fourth season's growth that differences in shoot growth could be detected in terms of dry weight. In contrast, with a rapidly growing *Salix* species planted under the same conditions, amendation significantly affected height growth over the first year, with differences among amendments being even more distinct when shoot weights were measured. With *Pinus banksiana* grown on oil sand tailings amended with the same materials (Parkinson et al., 1980), seedling heights in the four amendation treatments did not differ after the second growing season whereas up to 16-fold differences existed in shoot weights (unpublished data). In that there were very pronounced nutritional and microbial differences introduced to the spoils by the amendments described by Zak et al. (1982) and Grossnickle and Reid (1982) and the difficulties in detecting treatment effects by height growth with *Picea* and *Pinus* species, it is unlikely that a host response to inoculation would be detected by similar means. It would appear that destructive sampling will be necessary to evaluate inoculation trials in cold climates.

Due to slow host growth in mountainous or cool temperature climates, prolonged persistence of introduced symbionts is essential and this must be monitored to determine real effects of inoculation treatments. Grossnickle and Reid (1982) reported that neither *Pisolithus* or *Cenococcum* persisted on test plant root systems at a high elevation site in Colorado. Indeed, they estimated that infection of short roots in the waste material exceeded 50% in only one of the 12 mycorrhizal treatments after 4 years and in many cases was less than 20%. In that Marx et al. (1982) have estimated that infection by *Pisolithus* should exceed 50% to expect a growth response to inoculation, it is clear that long-term persistence and colonization of new roots represent key criteria for successful symbiont performance in sites with short growing seasons.

The effect of VA mycorrhizae on the growth of three legume species was evaluated on field plots established on a 10-year-old spoil bank by Lambert and Cole (1980). The acid spoil was amended with limestone and NH_4NO_3 and a minimal amount of topsoil (1 cm depth) to serve as VA inoculum. This inoculation treatment was highly effective as mycorrhizal infection was zero where no soil was added and exceeded 90% with soil additions. Both the growth and survival of all three species were markedly increased in the mycorrhizal treatments, e.g., survival after 3 years was improved 6-, 8-, and 15-fold for birdsfoot trefoil, crownvetch, and flat pea, respectively, with similar dry weight increases observed. In a separate experiment, phosphorus was shown to be limiting plant growth and that a combination of phosphorus fertilizer and topsoil resulted in better growth than when either one was applied separately. In the greenhouse, mycorrhizae did not result in improved growth of two grass species indicating that benefits may not be generalized for all species. Further, Lambert and Cole (1980) used five different vegetated mine spoils and a forest soil as inoculum for white clover in the greenhouse with their spoil adjusted to either pH 4.5 or 6.5. Although infection rates were similar among the inoculation treatments, yield response varied four-fold at pH 4.5 and five-fold at pH 6.5 with the different inocula. They considered these differences to indicate better adaptation to conditions in the acid spoil by some symbionts than by others. They concluded that the introduction of VA mycorrhizae to mine wastes would be useful if (1) inoculum is lacking or if the indigenous symbionts are ill-adapted, (2) if available phosphorus is low, and (3) if the plant species of choice respond to VA infection. The striking growth response of legumes demonstrated by Lambert and Cole (1980) appears to justify the time and expense of verifying if these conditions exist on other mine spoils.

Shrubs have received little attention in terms of mycorrhizal growth enhancement on mine spoils, and additional research appears to be warranted. Williams et al. (1974) determined that the growth of *Atriplex canescens*, a shrub native to arid regions in the southwestern United States, grew better in untreated soil than in autoclaved soil and suggested this was due to the VA mycorrhizal status of plants in the native soil. Lindsey et al. (1977) were unable to obtain infections of *Atriplex canescens* with extracted chlamydospores in coal spoil but demonstrated that another shrub, *Chrysothamnus nauseosus*, grew 13-fold better in autoclaved spoil inoculated with spores of *Glomus fasciculatus* than without inoculation and three-fold better in unautoclaved spoil when comparing inoculated and uninoculated materials. These greenhouse studies suggested that the growth and survival of woody shrubs might be enhanced on mine spoils in arid regions. Aldon (1978) demonstrated this by outplanting seedlings of *Atriplex canescens*, which had been inoculated with soil containing *Glomus mosseae*, onto a 4-year-old coal mine spoil. Uninoculated shrubs remained nonmycorrhizal, inoculated plants became infected, and shoot growth and survival of the latter were superior to nonmycorrhizal plants.

VA mycorrhizal tree species used on mine spoils may also benefit from inoculation. Inoculation of red maple in pots containing anthracite wastes stimulated growth when nutrients other than phosphate were supplied (Daft and Hacskaylo, 1977). Because VA mycorrhizal trees may grow well on mine spoils (Shuffstall and Medve, 1979), mycorrhizal dependencies and responses should be determined to provide information for management planning.

It has frequently been noted that some mine spoils may contain high levels of potentially toxic metals and this has led to repeated speculative statements that mycorrhizae might reduce toxicity and increase plant tolerance to contaminated soils or spoils. As stated previously, the data of Bradley et al. (1981, 1982) strongly suggest that mycorrhizal relationships are responsible for influencing patterns of plant colonization of sites characterized by high levels of available heavy metals. The colonization of metal contaminated and highly acid soils is characteristic of some ericaceous plants and Bradley et al. (1982) have argued convincingly that this colonization was related to complexing of the metals by the fungal element of ericoid mycorrhizae. Endophytes obtained from metal contaminated sites were no more beneficial to the host than an endophyte from natural heathland, perhaps as a consequence of high acidity and high availability of metals in undisturbed soils where ericaceous plants thrive (Bradley et al., 1981).

In contrast, VA mycorrhizal plants are usually found in less acid environments (e.g., agricultural soils) and not exposed to high levels of toxic metals. Bradley et al. (1982) state that colonization by grasses is rare on the same areas where *Calluna vulgaris* is common. However, VA mycorrhizal symbionts can become adapted to metal contaminated soils as Gildon and Tinker (1981) have shown. Copper and zinc were added to pots containing a clay loam soil and seeded with clover inoculated with either an isolate of *Glomus mosseae* from metal-contaminated soil or an isolate from an agricultural soil. Infection at all metal levels was greater with the isolate from the contaminated soil without associated increases in copper or zinc concentrations being observed in the plant tissue. Gildon and Tinker (1981) concluded that endophyte tolerance was important, implying that the mycorrhizal symbiont must be considered as a component of whole plant tolerance to potentially toxic metals. In a preliminary report, Killham and Firestone (1982) reported that under very acid conditions, a VA mycorrhizal grass accumulated higher levels of copper and nickel in the shoots than nonmycorrhizal plants, and that yield was reduced by mycorrhizal infection. Thus, it appears that infection by a VA fungus not adapted to heavy metals may have adverse effects on plant growth.

Whether ectomycorrhizae may impart tolerance to toxic metals has not been determined, but needles of pines infected with *Pisolithus* have been reported to contain lower levels of manganese and zinc (Berry, 1982) and manganese, iron, and aluminum (Marx and Artman, 1979) than plants infected with *Thelephora*. Heavy metal toxicity may have been the cause of the lack of mycorrhizae on *Salix* and *Populus* planted in copper mine tailings reported by Harris and Jurgensen (1977), although additional study indicated that the physiological condition of the host rather than copper toxicity prevented mycorrhizal formation (Jurgensen, 1978).

VI. CONCLUSIONS

Relatively few species of ectomycorrhizal symbionts have been identified as occurring on mine wastes, and of those, very few have been properly quantified with respect to their actual importance. To determine the degree of fungal symbiont adaptation to conditions on mine wastes, infection levels of each species must be quantified. It has been established that *Pisolithus tinctorius* is admirably adapted to spoil materials in warm climates, but in boreal and mountainous habitats it seems likely that other symbionts will be more effective and persistent. Research still remains largely concentrated on one symbiont although Parkinson (1979) warned of the dangers of directing all efforts on a single organism despite the enormous variety of mine waste habitats. Of the ectomycorrhizal symbionts listed as occurring spontaneously on spoils and tailings in Table 1, only *Pisolithus tinctorius, Thelephora terrestris,* and *Cenococcum geophilum* have been field tested successfully (Marx, 1980a). It is not possible to make decisions on species desirability for use in cold climatic regions until quantitative data on abundance and persistence of the various spontaneous or introduced symbiont colonizers are obtained and host performance in the field is evaluated. In other regions, *Pisolithus* is the obvious current choice and the standard with which other symbionts must be compared.

It appears that considerable strain differences exist among the VA fungi, and that it would be profitable to screen isolates for adaptability to mine spoils. It is likely that indigenous symbionts or those introduced with topsoil will not be those best adapted to mine sites (Lambert et al., 1980; Mosse et al., 1981). Old mine spoils with established vegetation may prove to be valuable sources of inoculum of adapted strains.

The general beneficial effect of the mycorrhizal condition on establishing and enhancing plant growth on mine wastes is evident. The principal mechanism appears to be improved mineral nutrition, although in special cases increased tolerance to toxic metals may be crucial. Plant inoculation is possible but in many cases it may not be justifiable, as in practice economic factors must be considered. If the main benefit is enhanced nitrogen or phosphorus uptake, inoculation must produce a "sustained improvement in plant performance so that it is superior to and more persistent than that obtained by phosphorus fertilization" (Lambert et al., 1980). Inoculation can more easily be justified in situations where inoculum is totally lacking or where nonnutrient stresses are decisive. Prior to any inoculation efforts, mine spoils, tailings, and any amending materials should be evaluated for mycorrhizal inoculum, as well as properties that affect plant growth and the potential benefits of embarking on a time consuming program of mycorrhizal manipulation.

Schramm's detailed examinations of the factors limiting plant establishment and success on mine spoils set the stage for employing one of the most common and essential links in disturbed ecosystems to repair the impacts of mineral and energy resources extraction. Although the potential value of mycorrhizae for improvement of disturbed site rehabilitation is appreciable, many problems must be considered and dealt with in an effective manner. Well-directed efforts must be guided by past observations and experiments to the end purpose of establishing both above-ground and below-ground processes that are both conducive to rehabilitating drastic disturbances to visually pleasing landscapes as well as establishing a recovery process that will persist after intensive management is completed.

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